

THE COELACANTH *RHABDODERMA* IN THE CARBONIFEROUS OF THE BRITISH ISLES

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ABSTRACT. Several points in the anatomy of *Rhabdoderma* are reinterpreted based on three-dimensional specimens from the Upper Carboniferous of Great Britain. It is shown that *Rhabdoderma* does not possess a basipterygoid process, and that the otico-occipital division of the braincase is completely ossified, with no trace of separate ossification centres. *Rhabdoderma* is distinguished from other coelacanths by the shape of the first dorsal fin support and the pattern of ornament on the scales. Emended diagnoses are given of the five British species considered as valid. *R.(?)abdenense* (Traquair) and *R.(?)davisii* Moy-Thomas are considered as belonging to *Diplocercides*. Species from the Carboniferous of North America and the Triassic of Madagascar are reviewed. The phylogenetic position of *Rhabdoderma* is discussed. The stratigraphical distribution of species of *Rhabdoderma* occurring in the British Isles is given. It is suggested that *Rhabdoderma* was euryhaline.

COELACANTH fishes from Carboniferous strata have long been known since their description by Agassiz (1844), Newberry (1856), Huxley (1866), Traquair (1881), and Davis (1883). In the British Isles at least, increasing exploitation of the coalfields led to the recognition of coelacanths as a dominant element in the Coal Measure fish fauna. Geological surveys and mining reports list many localities and numerous horizons at which coelacanths are found and, inevitably, a profusion of species has been named; some twenty species names have been used for Carboniferous coelacanths from the British Isles, but only a handful of these can be considered valid. Moy-Thomas (1935*a*, 1937) relegated many of the older species names to junior synonyms while, at the same time, he erected four new species. His 1937 paper provides the groundwork for the species recognition presented in this paper.

The geographic and stratigraphic distribution of Carboniferous coelacanths has hitherto been treated in piecemeal fashion; little attempt has been made to correlate the coelacanth occurrences with the very detailed stratigraphic literature available for Dinantian and Silesian rocks. The majority of coelacanth specimens occur in the Coal Measures, where they are found chiefly in the shales overlying the coal seams or in ironstone bands. Since individual coals are usually named, this means that specimens, even those in old collections, can be accurately located within the sequence. Only general statements about the stratigraphic and geographic distribution are offered in this paper, but a detailed breakdown, with references, is on file in the Department of Palaeontology, British Museum (Natural History).

The anatomy of Carboniferous coelacanths has been outlined most thoroughly by Huxley (1866) and Moy-Thomas (1937), but these works suffer from the fact that they antedated the discovery of the Recent model, *Latimeria*. Many cranial structures were difficult to interpret, and the problems of interpreting the Carboniferous fossils are particularly difficult because of preservation and the nature of the coelacanth skeleton. Most of the bones of the head lie separate from one another and must have been joined to one another by ligament or tough connective tissue, as in *Latimeria*. This, together with the fact that most Coal Measure coelacanths are flattened and often fragmentary, makes study of them particularly difficult. However, specimens from two localities, upper Culm Measures of north Devon and the Middle Coal Measures of north Staffordshire, are preserved as three-dimensional natural moulds, from which it is possible to make detailed rubber casts. By this means a great deal of new anatomical information can be obtained, and a summary is given here. A more detailed study will be published elsewhere, where extensive comparisons with other coelacanths can be given.

The primary objectives of this paper are therefore twofold: to update our knowledge of the anatomy and taxonomy of the Carboniferous coelacanths of the British Isles, and to collate information on the species from outside the British Isles.

Abbreviations preceding register numbers of specimens cited in this paper are as follows: BMNH—British Museum (Natural History), RSM—Royal Scottish Museum, SM—Sedgwick Museum, GN—Museum of Zoology, Cambridge University, FM—Field Museum of Natural History, MHNP—Muséum d'Histoire Naturelle, Paris, AMNH—American Museum of Natural History.

THE GENUS *RHABDODERMA*

Up to 1937 most authors grouped species of Carboniferous coelacanths in the genus *Coelacanthus* Ag., a genus founded on the Permian *C. granulatus* Ag., and which also included Triassic and Jurassic species (Woodward 1891). Moy-Thomas, however, reinstated a suggestion by Reis (1888, pp. 71–72) that the Carboniferous species should be separated as the genus *Rhabdoderma*. Reis pointed out that the Carboniferous species are distinguishable by a well-developed ornamentation of closely spaced ridges and tubercles on the scales, lower jaw, and gular plates. To this Moy-Thomas was able to add further features by which the Carboniferous species differed from the type-species of *Coelacanthus*: these included the presence in *Rhabdoderma* of a triangular coronoid (versus rectangular), a basiptyergoid process (absent in *C. granulatus*), and the absence in *Rhabdoderma* of ossified ribs and the presumed absence of an extracleithrum (both present in the Permian species). But these additional features, while enabling *Rhabdoderma* to be distinguished from *C. granulatus*, do not allow it to be distinguished from other coelacanth genera. For example, a triangular coronoid is present in *Wimania*, a basiptyergoid process is present in *Diplocercides*, ossified ribs are absent from most coelacanths, and the extracleithrum is absent from *Macropoma*. In other words, these character states are not synapomorphies for the recognized species of *Rhabdoderma*. Furthermore, in two features (the presence of a basiptyergoid process and the absence of an extracleithrum) previous statements and interpretation have to be modified (pp. 206, 211). But there do seem to be two features peculiar to *Rhabdoderma*; scales bearing an ornament of ridges which converge to the midline of the scale (Reis 1888) and the kidney-shaped endochondral support of the first dorsal fin (Schaeffer 1941). A definition of *Rhabdoderma* incorporating these features would also reflect the primitive position of the genus amongst coelacanths (p. 224).

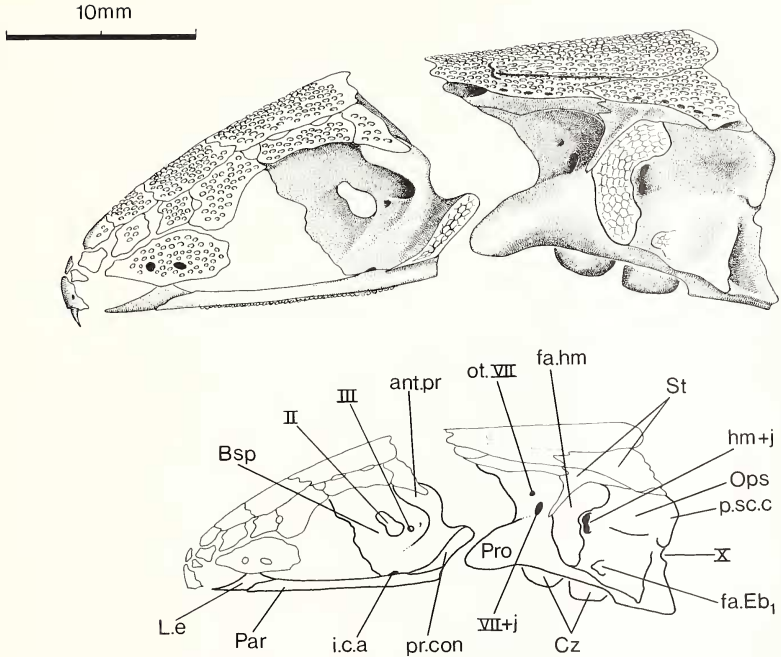
Definition. Primitive coelacanth which retains broad, partially overlapping cheek bones which form a complete covering behind the eye, a postspiracular and suboperculum present, a preorbital (antorbital of authors) perforated by the posterior openings of the rostral organ: premaxilla carrying the ethmoid commissure; pitlines marking the parietal, squamosal, preoperculum, angular, and gular plate: five extrascapulars: ethmosphenoid moiety of braincase in which the interorbital septum is partially ossified and paired lateral ethmoids (ectethmoids) present: otic division of braincase extensively ossified; descending lamina of supratemporal present but parietal lamina absent: pectoral girdle with ornament restricted to the dorsal half of the cleithrum: pelvic fin inserting behind the level of the first dorsal fin: ossified ribs absent: support of anterior dorsal fin kidney-shaped: primary rays of the caudal fin with a one-to-one relationship with the endochondral supports: lepidotrichia of all fins smooth and without ornament: air bladder, where known, with calcified walls: scales ornamented with ridges and tubercles which converge posteriorly.

Type species. *Rhabdoderma elegans* (Newberry 1856), Westphalian D, Linton, Ohio.

Anatomy

The anatomy of the genus *Rhabdoderma* is most completely known from the type-species. As pointed out below (p. 212) the differences between the species primarily concern differences in ornamentation and meristic counts, so the remarks made here may be taken as being relevant to all species except where otherwise indicated.

The braincase (text-fig. 1), as in all coelacanths, is divided into two moieties, an ethmosphenoid and an otico-



TEXT-FIG. 1. *Rhabdoderma elegans* (Newberry)—restoration of the braincase based on BMNH P.7912, P.10437 and SM E.169. The two moieties of the braincase have been drawn as if pulled slightly apart. Abbreviations: ant.pr—antotic process, Bsp—basisphenoid, Cz—catazygal, fa.hm—facet for hyomandibular, fa.Eb₁—facet for articulation of epibranchial 1, hm+j—foramen for hyomandibular branch of facial+jugular vein, i.c.a— foramen for internal carotid artery, L.e—lateral ethmoid, Ops—opisthotic region, ot.VII— foramen for otic ramus of facial, Par—parasphenoid, pr.con—processus connectens, Pro—prootic region, p.sc.c—ridge marking position of posterior semicircular canal, St—supratemporal, II— foramen for optic tract, III— foramen for oculomotor, VII+j— foramen for facial+jugular vein, X— foramen for vagus.

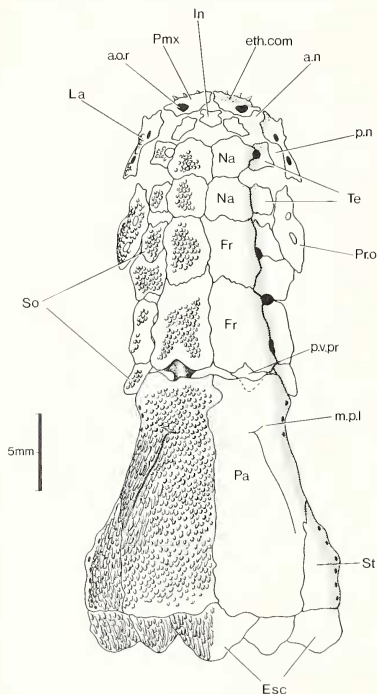
occipital, which are separated by the characteristically complex intracranial joint (intracranial juncture apparatus, Bjerring 1973). The coelacanth intracranial joint has three basic skeletal components: dorsally there is a sliding portion between postero-ventral processes (p.v.pr) of the frontals (Fr) and the undersurface of the parietals (Pa), ventrally there is an articulation between the sphenoid condyles on the posterior face of the basisphenoid (Bsp) and the anterior face of the anazygal; laterally there is a further sliding joint between the processus connectens (pr.con) of the basisphenoid and a groove on the inside of the prootic (Pro). In *Rhabdoderma* the dorsal sliding portion is poorly developed and the postero-ventral processes of the frontals are very short (text-fig. 2). This is a primitive coelacanth feature also seen in *Diplocercides* (incl. *Nesides*, p. 218) and is probably related to the fact that in these coelacanths the basisphenoid extends far dorsally to contact the skull roof. The sphenoid condyles are also poorly developed but the processus connectens (text-fig. 1) with the

corresponding groove on the prootic is very long, reaching anteroventrally from the sphenoid condyle to the contact between the basisphenoid and the parasphenoid (Par). In this respect *Rhabdoderma* is similar to *Coelacanthus* and *Laugia*, but differs from more advanced coelacanths such as *Macropoma*, *Holophagus*, and *Latimeria*, in which the processus connectens is relatively short.

The endochondral ossifications of the ethmosphenoid (text-fig. 1) consist of paired lateral ethmoids (L.e) anteriorly and a large unpaired basisphenoid posteriorly. I have nothing further to add to Moy-Thomas' description of the lateral ethmoid as 'more or less triangular in shape in the horizontal plane' (1937, p. 388).

The basisphenoid, however, needs comment since it has been differently restored by Moy-Thomas and Aldinger (1931, fig. 15). Aldinger's specimen, named by him as *Coelacanthus* sp., has been referred to *Rhabdoderma* (?) *aldingeri* by Moy-Thomas (1937), but there is no good reason for associating this form with *Rhabdoderma*, and certain features suggest that it should be more appropriately allied with *Diplocercides* (see p. 219).

Moy-Thomas (1937, fig. 3) restores a short basisphenoid in a large individual (BMNH P.7912), somewhat similar to that described for *Wimania* by Stensiö (1921). However, this is certainly wrong, at least in this and other large specimens. BMNH P.10473, for instance, shows clearly a basisphenoid with pronounced anterior laminae which form a partially ossified interorbital septum (text-fig. 1) similar to that figured by Aldinger. The septum is pierced anteriorly by a large optic foramen (II) and behind this there is a small oculomotor foramen (III). The antotic process (ant.pr) is well developed as a lateral projection immediately beneath the skull roof, and at the base of this process lies the profundus foramen. It is impossible to identify foramina for the trochlear



TEXT-FIG. 2. *Rhabdoderma elegans* (Newberry)—restoration of the skull roof based on several specimens in the BMNH and AMNH. Path of sensory canals and pitlines shown on right side, ornament shown on left. Abbreviations: a.n—anterior nostril, a.o.r—anterior opening for rostral organ, Esc—extrascapular, eth.com—ethmoid commissure, Fr—frontal, In—internasal, La—lacrimal, m.p.l—middle pit-line, Na—nasal, Pa—parietal, Pmx—premaxilla, p.n—posterior nostril, Pr.o—preorbital, p.v.pr—posteroventral process of frontal, So—supraorbital, St—supratemporal, Te—tectal.

nerve and the pituitary vein, which often perforate the basisphenoid. It is possible that the degree of ossification of the basisphenoid is related to age; this is certainly the case in *Laugia*, where a growth series is available.

As mentioned above, the processus connectens is very long and flanks the concave posterior face of the basisphenoid. Moy-Thomas shows the processus connectens as turning horizontally where it meets the basisphenoid, and he interprets the horizontal portion as a basiptyergoid process. I cannot confirm this observation or interpretation on the specimen used by Moy-Thomas, or on other specimens in the BMNH (e.g. BMNH P.6613a, P.6663), and it must be regarded with suspicion. In *Diploceirides* the basiptyergoid process is an independent knob-like structure, anterior and slightly dorsal to the anterior tip of the processus connectens (Jarvik 1954, fig. 4), exactly as Aldinger figured it for his *Coelacanthus* sp. I therefore reject the identification of a basiptyergoid process in *R. elegans*. I have not seen a basiptyergoid process in any other species here referred to *Rhabdoderma*.

The parasphenoid (Par) is closely applied, but never fused (cf. Moy-Thomas 1937), to the base of the basisphenoid (text-fig. 1). Anteriorly it expands but remains a flat plate without the dorsal processes seen, for instance, in *Macropoma*. The parasphenoid is said by Moy-Thomas to be wider in *R. tingleyense* than in *R. elegans*, but relative width appears to increase throughout the growth of the individual and it is therefore of doubtful use in species identification. Teeth are borne over most of the ventral surface, and this primitive feature, and the long processus connectens, suggest that the basicranial muscle was probably short, as in other primitive coelacanths, and had its anterior insertion along the posterior edges of the basisphenoid and the parasphenoid (see Bjerring 1967 for a fuller discussion of the length of the basicranial muscle in coelacanths).

The roofing bones of the ethmosphenoid portion of the braincase are arranged in typical coelacanth fashion (text-fig. 2) with two longitudinal series of paired bones, an inner frontonasal series of five (cf. Moy-Thomas 1937, fig. 1), and an outer supraorbito-tectal series of seven. Wedged between the anterior tectal of either side there is a small median internasal (In) (postrostral or inter-rostral) and in front of these lie the paired premaxillae (Pmx). The premaxilla is a single element perforated by the anterior opening of the rostral organ (a.o.r) and the ethmoid commissure (eth.com). This is a primitive feature in adult coelacanths. In more derived coelacanths such as *Latimeria*, *Diplurus* (see Schaeffer 1952), *Undina cirinensis* (see Saint-Seine 1949), and possibly *C. granulatus* (see Schaumburg 1978) the tooth-bearing bone(s) is separated from the canal-bearing elements, the latter being called rostrals. The otico-occipital division of the braincase is roofed by paired parietals (intertemporals), supratemporals (St), and a transverse chain of five extrascapulars (Esc) (text-fig. 2).

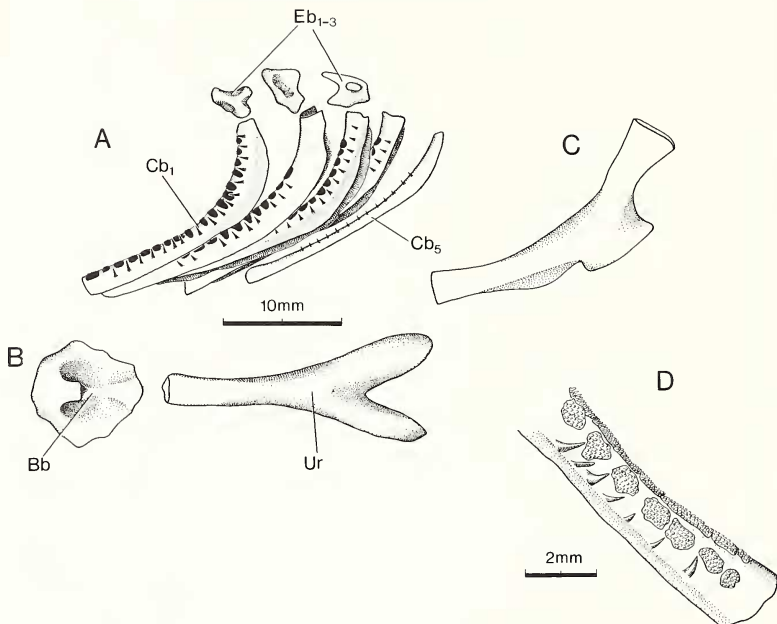
The otico-occipital division of the neurocranium (text-fig. 1) is extensively ossified, and the interpretation given here differs considerably from that by Moy-Thomas, who used a single, distorted specimen (BMNH P.7912). He based his interpretation of this specimen on the model of the coelacanth braincase proposed by Stensiö (1921), and came to the conclusion that there were three paired and two median elements, separated in life by cartilage.

Two specimens of *R. elegans* show the otic region particularly clearly; BMNH P.10473, a large individual, and SM E. 169, a small one. Both show the otic and occipital areas covered by a continuous sheet of bone, the only independent elements being the zygal, which lie in the ventral mid-line and which, incidentally, may clearly be seen in BMNH P.7912, the specimen used by Moy-Thomas. Of course it is very likely that the otico-occipital division of the neurocranium did ossify from several centres, since it is difficult to imagine how else it could have grown, but there is no clear evidence of these separate centres, except possibly an independent supraoccipital.

A restoration of the otico-occipital region is given in text-fig. 1, and several features may be pointed out. The prootic region is well ossified; it extends dorsally to contact the skull roof, and it is probably because of this that a descending lamina of the parietal ('apophyse descendante de l'os intertemporal' of Millot and Anthony 1958) is absent. A descending process from the supratemporal is present (text-fig. 1) and this lies along the anterior edge of the hyomandibular facet (fa.hm) which, as usual, is a very large, bilobed, cartilage-capped area lateral to the combined jugular canal and the exit of the hyomandibular nerve (hm + j). Behind the hyomandibular facet there are two shallow depressions, one above the other; the upper represents the insertion site of the adductor opercularis, the lower the insertion for the adductor hyomandibularis. The point of articulation of epibranchial I (fa.Eb₁) can be recognized as an area of exposed endochondral bone posterior to the lower end of the hyomandibular facet.

An interrupted ridge (text-fig. 1) runs vertically at the posterior limit of the otic region and this marks the anterior limit of the insertion of epaxial trunk musculature. Mid-way down this vertical ridge there is a well-developed postotic process which is the site of origin for branchial levators 1-4, and immediately below this lies the vagus foramen. The second epibranchial articulates with the braincase at the ventral tip of the vertical ridge. Behind this level the occipital portion of the braincase remains largely unknown. The impression of a median butterfly-shaped element is preserved in BMNH P.7912, which corresponds to a similar-shaped bone in *Laugia*, *Holophagus*, and *Macropoma*, and this may represent a supraoccipital.

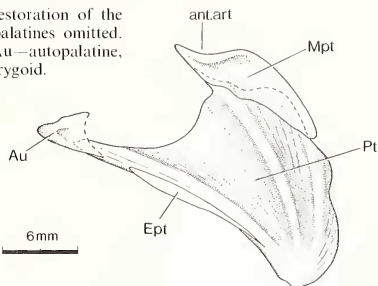
In all, the otico-occipital region of the braincase shows several primitive coelacanth characteristics: it is extensively ossified and reaches the dermal roof, there are no obvious sutures within the neurocranium and a parietal bracing strut is absent. It is more advanced than that of *Diplocercides*, where a descending lamina of the suprtemporal is also absent, but more primitive than that of *Laugia* which, while also showing an extensively ossified otico-occipital region, retains sutures between growth centres throughout life.



TEXT-FIG. 3. *Rhabdoderma elegans* (Newberry) — gill arches. A. Restoration of the branchial arches in left lateral view. B. Restoration of the basibranchial and urohyal in ventral view. C. Ceratohyal. D. Camera-lucida drawing of the lower end of second ceratobranchial in right lateral view to show shape and position of the three rows of tooth plates, BMNH P.10473. Abbreviations: Bb — basibranchial, Cb₁ — ceratobranchial 1, Cb₅ — ceratobranchial 5, Eb₁₋₃ — epibranchials 1-3, Ur — urohyal.

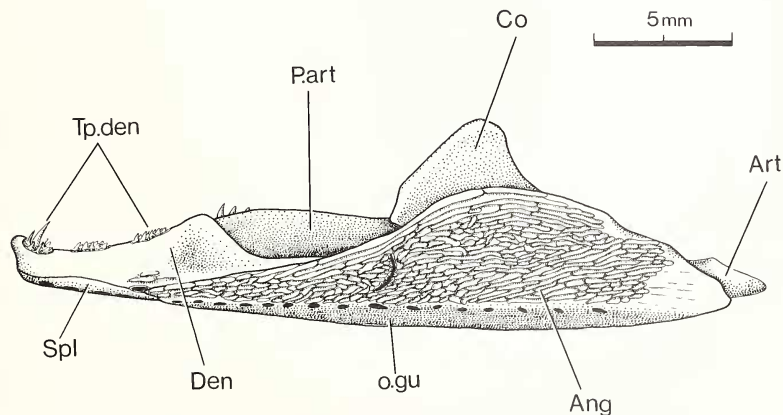
The gill arches are unremarkable for a coelacanth and may closely approach the conditions expected in a primitive osteichthyan. There are five arches (text-fig. 3), the dominant element in each being the ceratobranchial (Cb). Separate hypobranchials are unknown but the first three arches at least bear ossified epibranchials (Eb). Ventrally there is a large basibranchial (Bb), to which are attached the first three arches. The ceratobranchials bear three rows of tooth-plates (text-fig. 3D), the outer or anterior row being specialized as gill-rakers (the 'conodonts' of Demanet 1939). The basibranchial dentition is incompletely preserved but there is a pair of anterior tooth-plates. Paired basibranchial plates are primitive for osteichthyans (Nelson 1969) and many coelacanths show three pairs of large plates corresponding to the first three gill arches. The ceratohyal (text-fig. 3C) is typical for a coelacanth.

TEXT-FIG. 4. *Rhabdoderma elegans* (Newberry)—restoration of the palate in left lateral view. Quadrate and dermopalatines omitted. Abbreviations: ant.art—antotic articulation, Au—autopalatine, Ept—ectopterygoid, Mpt—metapterygoid, Pt—pterygoid.



The palate (text-fig. 4) is unremarkable for a coelacanth. The pterygoid (Pt) bears three strengthening ridges which radiate from the quadrate region (a separate quadrate is not seen in specimens of *Rhabdoderma* and may well have been represented by cartilage only). The visceral surface of the pterygoid is covered with a shagreen of teeth which tend to be arranged in whorls posteriorly. There are dermopalatines lying anterior to the ectopterygoid, but they are not sufficiently well known to allow their restoration.

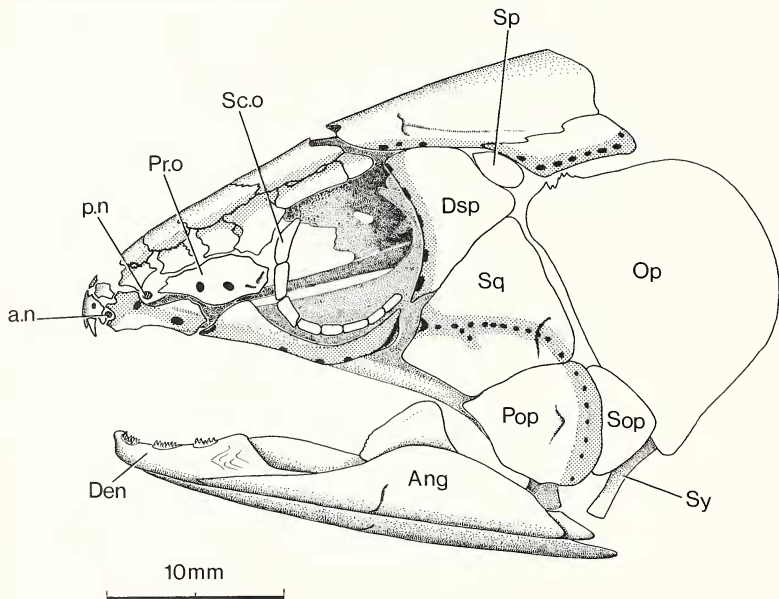
The lower jaw (text-fig. 5) is also similar to that of most other coelacanths, with a large angular (Ang) and small splenial (Spl) which carry the mandibular sensory canal, and a very small dentary (Den). As in most coelacanths the dentary bears separate tooth-plates (Tp.den) and the teeth on the anterior tooth-plate are relatively large. The triangular coronoid (Co) is an unusual feature of the genus but not unique among coelacanths. The posterior end of Meckel's cartilage is ossified as a single ossification, the articular (Art), in contrast to the two ossifications set in tandem in *Latimeria* and *Macropoma*. The articular has two articulatory facets, the anterior one for the quadrate, the posterior for the symplectic (Sy). Indeed, this unusual type of double jaw articulation is seen in all coelacanths (cf. Schaeffer 1941, p. 16) in which the lower jaw is known.



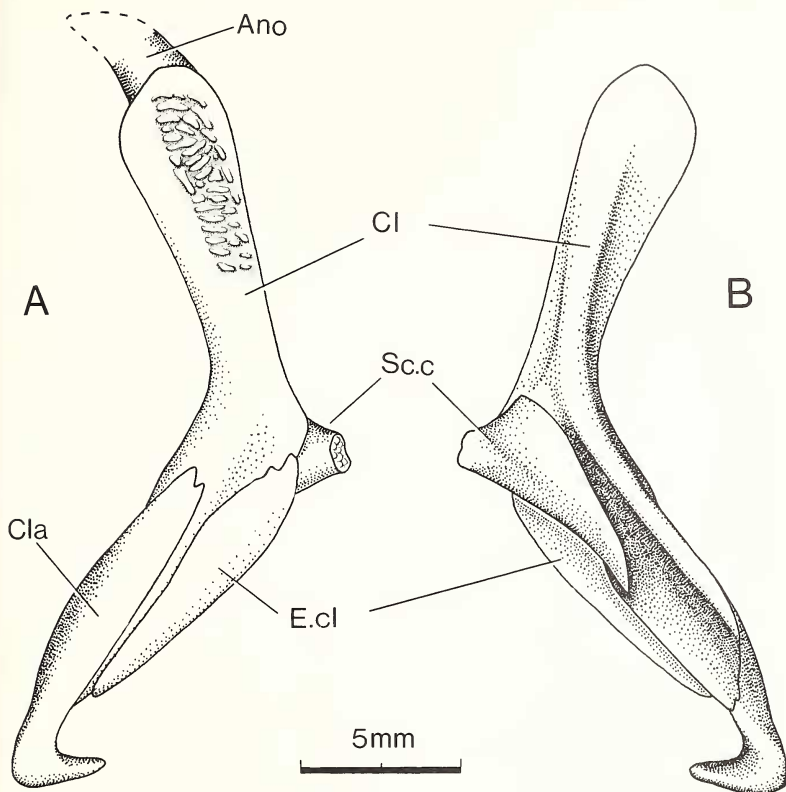
TEXT-FIG. 5. *Rhabdoderma elegans* (Newberry)—restoration of the lower jaw in left lateral view. Based on several specimens in the BMNH and RSM. Abbreviations: Ang—angular, Art—articular, Co—coronoid, Den—dentary, o.gu—overlap area for gular, Part—prearticular, Spl—splenial, Tp.den—dentary tooth plate.

The circumorbital and cheek bones (text-fig. 6) fit closely together and there are overlap areas between the dermosphenotic (Dsp) (postorbital) and squamosal (Sq) and between the squamosal and preoperculum (Pop) (quadratojugal). The latter bone largely overlaps the suboperculum (Sop). This appears to be a feature of primitive coelacanths, as does the persistence of grooves for the vertical pitline of the cheek. The orbit is bordered anteriorly by a large preorbital (Pro) (antorbital) and this is perforated by two holes for the dorsal and ventral posterior openings of the rostral organ (p.o.r). Elsewhere the preorbital is seen in *Whiteia* and *Spermatodus* but it is absent from more advanced coelacanths.

The postcranial skeleton has, in large part, been satisfactorily described by Moy-Thomas (1937) and discussed by Schaeffer (1941); it is illustrated here in text-fig. 9, where the obvious features may be seen. The characteristic shape of the first dorsal fin support has already been noted and it is only necessary to comment upon the pectoral fin and girdle. The restoration of the girdle given by Schaeffer (1941, fig. 5c) differs considerably from that given here (text-figs. 7, 8). An anocleithrum (Ano) (supracleithrum) is known, albeit incompletely, from BMNH P.10473. The clavicle (Cla) is produced ventrally as a flat horizontal portion which probably contacted its partner in the ventral mid-line. Both these features are very similar to those seen in *Latimeria*, *Macropoma*, *Whiteia*, and *Laugia*, and it is probable that on further investigation this feature will be seen in all coelacanths. In primitive actinopterygians, osteolepiforms, primitive lungfish, and tetrapods there is a small interclavicle wedged between the clavicles of either side. In *Laugia*, *Whiteia*, and *Macropoma* among coelacanths the interclavicle has sunk beneath the surface to lie above the clavicles. It is therefore probable that *Rhabdoderma* also possessed an interclavicle, but I have been unable to identify it in any specimen examined.



TEXT-FIG. 6. *Rhabdoderma elegans* (Newberry)—restoration of the skull in left lateral view. Proportions of the skull bones based on BMNH P.6286. Abbreviations: a.n.—anterior nostril, Ang—angular, Den—dentary, Dsp—dermosphenotic, Op—operculum, p.n.—posterior nostril, Pop—preoperculum, Pro.—preorbital, Sc.o.—sclerotic ossicle, Sop—suboperculum, Sp—spiracular bone, Sq—squamosal, Sy—symplectic.

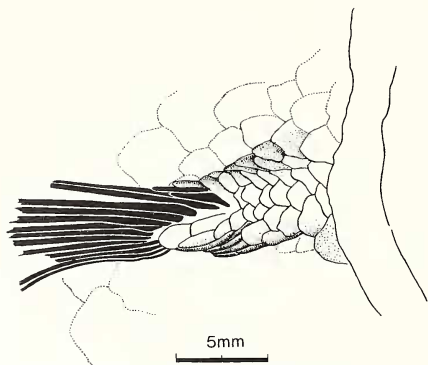


TEXT-FIG. 7. *Rhabdoderma elegans* (Newberry)—restoration of the pectoral girdle in A, lateral and B, medial views. Abbreviations: Ano—anocleithrum, Cl—cleithrum, Cla—clavicle, E.cl—extracleithrum, Sc.c—scapulocoracoid.

A separate extracleithrum (E.cl) is said to be absent in *Rhabdoderma* and indeed in most specimens it cannot be seen. But BMNH P.57973 and P.10474 show a large scale-like extracleithrum lying separate from the girdle, while in BMNH P.10473 and AMNH 9589 it lies along the posterior edge of the ventral shank of the cleithrum (Cl). It is clear, however, that it is not closely associated with the cleithrum, since that bone shows no clear overlap surface. It is possible that the extracleithrum is not present in all individuals.

The endoskeletal shoulder girdle is represented as an independent triangular scapulocoracoid (Sc.c) (cf. Moy-Thomas 1937, p. 395). It rests against the inner surface of the cleithrum, and it is probable that there was a large expanse of cartilage fitting into a deep groove in the cleithrum as in *Latimeria* (Millot and Anthony 1958, fig. 25). The distal end of the scapulocoracoid was also capped by cartilage.

Nothing is known of the endoskeleton of the pectoral fin. BMNH P.10473 shows that the fin was pedunculate (text-fig. 8) as in *Latimeria*, rather than lobed. This has some significance since Berg (1940) assigned *Latimeria* to the monotypic family Latimeriidae on this feature. Consequently the separation of *Latimeria* from other coelacanths on this criterion cannot be maintained.



TEXT-FIG. 8. *Rhabdoderma elegans* (Newberry)—pectoral fin base of right side. Camera-lucida drawing of BMNH P.10473.

The above notes on the anatomy of *Rhabdoderma* are given as both a supplement and an emendation to the work of Moy-Thomas and Huxley. They show that *Rhabdoderma* is a primitive coelacanth differing from the Devonian *Diplocercides* in only a few derived features: reduced ossification of the ethmosphenoid, presence of a descending lamina of the supratemporal, loss of the basipterygoid process (this is present in Aldinger's *Coelacanthus* sp., see p. 207 and has been reported in *Synaptotylus*, see p. 220), and in having the dentary teeth separate from the supporting bone.

SPECIES OF *RHABDODERMA* OCCURRING IN THE BRITISH ISLES

In this section the species of *Rabdoderma* are listed together with diagnoses where the latter can be usefully emended from those given by Moy-Thomas (1935a, 1937). Stratigraphic and geographic distribution is deferred until a following section. Despite the wealth of material from the Coal Measures, specific distinction still centres on differences in ornamentation, although this is known to be variable. All told, some twenty species have been recognized from the Carboniferous of the British Isles and most of these have been established on the basis of so-called distinctive ornament of scales, isolated gulars, or operculae. Many of these species are best interpreted as variants of *R. elegans* or *R. tingleyense*. Moy-Thomas gives a good review, with references, of many of these species and, rather than repeat lengthy synonymy, the reader is referred to his work. Table 1 lists the species recognized in this paper with synonyms. For comparative purposes, illustrations are included of the ornament pattern on the scales of most of the species recognized here (text-fig. 10). In the diagnoses the following abbreviations have been used: D₁—anterior dorsal fin, D₂—posterior dorsal fin, C—caudal fin, A—anal fin, P—pectoral fin, V—pelvic fin.

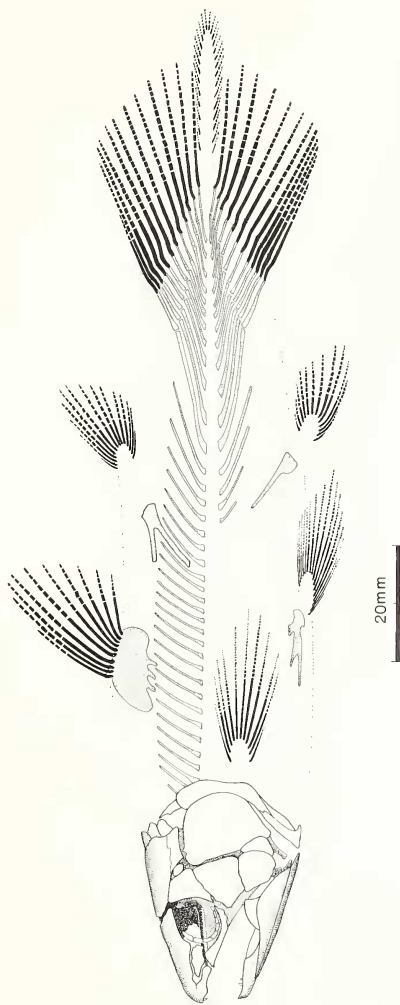
TEXT-FIG. 9. *Rhabdoderma elegans* (Newberry)—restoration of entire skeleton.

TABLE 1. Species of *Rhabdoderma* and other Carboniferous coelacanths recognized in this paper

THIS PAPER	SYNONYMS
<i>R. elegans</i> (Newberry 1856)	<i>Coelacanthus lepturus</i> Ag. 1844—undefined, <i>Holophagns binneyi</i> Ag. 1844—undefined, <i>Coelacanthus robustus</i> Newberry 1856, <i>Coelacanthus ornatus</i> Newberry 1856, <i>Conchiopsis filiferus</i> Cope 1873, <i>Conchiopsis anguliferus</i> Cope 1873, <i>Coelacanthus elongatus</i> Huxley 1866, <i>Coelacanthus summiti</i> Wellburn 1903, <i>Coelacanthus watsoni</i> Aldinger 1931, <i>Rhabdoderma corrugatum</i> Moy-Thomas 1935a, { <i>Coelacanthus newelli</i> Hibbard 1933, <i>Coelacanthus arcuatus</i> Hibbard 1933, <i>Coelacanthus mucronatus</i> Pruvost 1913, <i>Coelacanthus granulosistriatus</i> Moy-Thomas 1935a <i>Coelacanthus phillipsi</i> Ag. 1844.
Possibly <i>R. elegans</i>	
<i>R. tingleyense</i> (Davis 1884)	
Possibly <i>R. tingleyense</i>	
<i>R. luxleyi</i> (Traquair 1881)	
Possibly <i>R. luxleyi</i>	<i>Rhabdoderma(?) alderingi</i> Moy-Thomas 1937
<i>R. arrossense</i> Moy-Thomas 1937	
<i>R. madagascariensis</i> (Woodward 1910)	
<i>Diplocercides davisii</i> (Moy-Thomas 1937)	<i>R.(?) davisii</i> Moy-Thomas 1937 <i>R.(?) abdenense</i> Moy-Thomas 1937 <i>Coelacanthus</i> sp. Aldinger 1931, <i>Coelacanthus welleri</i> Eastman 1908, <i>Coelacanthus exiguus</i> Eastman 1902, <i>Coelacanthus hindi</i> Wellburn 1902b, <i>Coelacanthopsis curta</i> Traquair 1905, <i>Coelacanthus distans</i> , <i>C. woodwardi</i> , <i>C. tuberculatus</i> , <i>C. spinatus</i> , all named without definition by Wellburn 1902a. <i>Rhomboderma gorskyi</i> Chabakov 1927.
<i>Diplocercides</i> sp.	
Possibly <i>Diplocercides</i>	
Coelacanth indet.	
Indeterminate remains	

Rhabdoderma elegans (Newberry)

For synonymy see Moy-Thomas (1937); add *R. corrugatum* (Moy-Thomas 1935a).

Diagnosis (emended). *Rhabdoderma* reaching 400 mm, but most specimens less than 250 mm; D₁ 10; D₂ 14 or 15; C 12–13 in both the upper and lower lobes; A approximately 13; P 11; V 14–16; approximately 40 neural arches and spines between the shoulder girdle and the base of the middle caudal lobe; approximately 55 vertical scale rows anterior to the base of the middle caudal lobe; roofing bones of the skull ornamented with ovoid tubercles arranged irregularly; cheek bones and angular with elongate tubercles surrounded by ridges which parallel the margins, gular plate with parallel ridges which converge anteriorly; ornament on scales consisting of adjoining ridges which converge posteriorly.

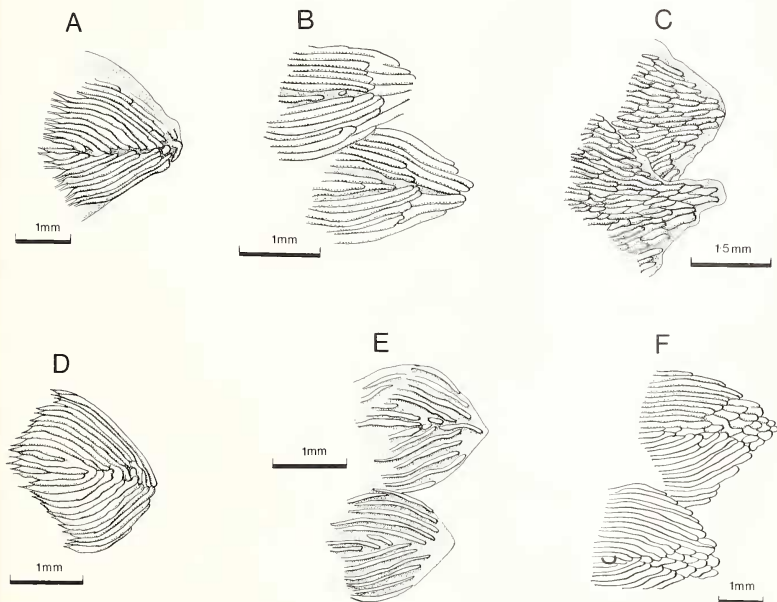
Remarks. Moy-Thomas (1935a, 1937) pointed out that the detailed pattern of ornamentation varies considerably from specimen to specimen. This variability accounts for a great number of species placed in synonymy by Moy-Thomas. A few generalizations about this variability can be made. In small individuals (under 80 mm) the tubercles on the skull roof are sparse and the cheek and opercular bones generally have tubercles only, the marginal ridges being added with further growth. On the scales, the initial ornamentation consists of ridges but, as the scale grows, it is quite common to find tubercles: that is, the ridges appear to break up towards the margin. They nevertheless remain parallel

to the margin of the scale. In some specimens the posterior tip of the scale is drawn out into a short 'tail' which was held to be the distinguishing characteristic of *C. mucronatus* Pruvost (1913), correctly placed in synonymy with *R. tingleyense* by Moy-Thomas. The specimens described by Moy-Thomas as *R. corrugatum* are all fragmentary remains of small individuals, the shape and ornamentation of which agree well with small specimens of *R. elegans*. Approximately eighty specimens were examined in this study.

Rhabdoderma tingleyense (Davis)

For synonymy see Moy-Thomas (1937); add *R. (?) granulostriatum* (Moy-Thomas 1935a).

Diagnosis (emended). *Rhabdoderma* reaching 450 mm; D₁ 15; D₂ 16; C 21–23 in both upper and lower lobes; P approx. 17; V approx. 18; external bones of skull (except gular) ornamented with closely spaced, slightly elongated tubercles; gulars with parallel ridges and elevated tubercles, sometimes granular; scales with many closely packed tubercles which in some specimens are aligned longitudinally.



TEXT-FIG. 10. *Rhabdoderma*—camera-lucida drawings to show ornament patterns on exposed surfaces of the scales from five species. A. *R. elegans* (Newberry), large individual, BMNH 36477. B. *R. elegans* (Newberry), small individual, BMNH 21464. C. *R. tingleyense* (Davis), BMNH P.1188. D. *R. ardressense* Moy-Thomas, BMNH P.19244. E. *R. huxleyi* (Traquair), BMNH P.4080a. F. *R. madagascariensis* (Woodward), MHNP 1972-7. In all except E, examples have been drawn from scales lying near the mid-line between the two dorsal fins. E. represents a scale from immediately behind the pectoral fin.

Remarks. *R. tingleyense* is very similar to the type-species and there is no doubt that in most collections identifications have been confused, and often the condition of preservation does not allow them to be separated. There are considerable meristic differences (see above) but, as most material is unsuitable for their determination, ornamentation is still the most practical criterion. As in *R. elegans* there is some variability, but generally the ornamentation consists entirely of tubercles except on the gulars. The difference in the ornament is better illustrated than described and may be seen by comparing text-fig. 10A, B, *R. elegans* with text-fig. 10C, *R. tingleyense*. One interesting variant of ornamentation occurs on the gular plate, which in some specimens (e.g. BMNH P.57951) is granular and is similar to that described as *R.(?) granulostriatum*. For this reason the latter species is placed as a junior synonym of *R. tingleyense*. I cannot confirm Moy-Thomas' (1937, p. 403) claim that the frontals are as long as the parietals; instead they seem to be about half the length, as in *R. elegans*. Approximately sixty specimens were examined in this study.

Rhabdoderma luxleyi (Traquair 1881)

For synonymy see Moy-Thomas 1937.

Diagnosis (emended). *Rhabdoderma* reaching 160 mm; D₁ 9–10; D₂ 10–11; C 16–17 in upper lobe, 15–16 in lower lobe; P at least 8; approximately forty neural arches and spines between shoulder girdle and base of middle caudal lobe; ornament absent from roofing bones of the skull and from the operculum; ornament upon angular and gular consisting of a few, widely spaced ridges; scales ornamented with narrow, sometimes broken, ridges which are well separated from one another.

Remarks. In addition to the specific distinguishing characteristics mentioned above, *R. luxleyi* is unusual among *Rhabdoderma* species in a number of other features. Within the otic region the otoliths ('conspicuous humps' of Moy-Thomas 1937, p. 405) are often preserved. They are similar in shape to those of adult *Latimeria* but are relatively much larger; in *R. luxleyi* the ratio of otolith length to the length of the parietal shield is 1:1.8; for *Latimeria* this is 1:3.25. This could be interpreted as a juvenile characteristic, an idea which gains support from the fact that the median lobe of the caudal fin is relatively long, 20% of the total length in a fish of 75 mm (P.4080a) and 15% total length in a fish of 100 mm (BMNH P.4080b). A very long middle caudal lobe is recorded in the larval form, *C. exiguum* Eastman, by Schultz (1972). *Latimeria* also shows a proportionately longer middle caudal lobe in the young. Unfortunately we know nothing of the relative sizes of the otoliths in other extinct coelacanths or, as yet, in young *Latimeria*, and the view that *R. luxleyi* is a juvenile form must be balanced by the fact that ossification seems advanced and that there are no large specimens from the same locality. The parietal shield is short relative to the fronto-ethmoid shield (1:2) and this contrasts with a ratio of 1:1.3 in *R. elegans* and *R. tingleyensis*. The cleithrum is also unusual; the posterior margin below the fin insertion is expanded and rounded. A final distinctive feature is the pectoral fin-rays, which are segmented right to their bases, whereas in other species segmentation is limited to the distal two-thirds. Eleven specimens were examined in this study.

Rhabdoderma (?) aldingeri Moy-Thomas 1937

For synonymy see Moy-Thomas (1937).

Remarks. This species is based on a single specimen (GN 241), which consists of a crushed head plus anterior part of the trunk. It comes from Namurian A (*Emnorphoceras bisulcatum* zone) of Tryddyn Church, Clwyd. It has been described by Moy-Thomas who includes a photograph (1937, pl. 3). The specimen is very poorly preserved and few details can be seen. Moy-Thomas compared this specimen with Aldinger's *Coelacanthus* sp., but there seems very little similarity between these two. GN 241 shows an operculum which is perfectly smooth, without ornament (*Coelacanthus* sp. has a tuberculated operculum). The gular is ornamented with fine, well-spaced ridges (Moy-Thomas 1937, fig. 15) and the scales, which are very thin, appear to have a few scattered ridges. These three features are found in *R. luxleyi* and it is possible that *R. (?) aldingeri* should be considered a junior synonym.

Rhabdoderma ardrossense Moy-Thomas 1937

Diagnosis (emended). *Rhabdoderma* known only from the holotype and BMNH P.22005-6: D₁ 10; D₂ 10; C 18 in upper lobe, 17 in ventral lobe; 45 neural arches and spines between shoulder girdle and middle caudal lobe; external bones of the skull ornamented with a few coarse ridges; scales bearing adjoining ridges (text-fig. 10D) which converge posteriorly and are very similar to those of young *R. elegans*.

Remarks. The larger of the two specimens, the holotype, measures 117 mm total length. The head of the holotype was figured by Moy-Thomas (1937, pl. 3) in which the characteristic ornament is well shown. However, it should be pointed out that the bone labelled angular is, in fact, the gular of the right side which almost completely covers the angular. The two bones may be distinguished in Moy-Thomas's plate by the slight change in the orientation of the ornament ridges.

Coelacanthus phillipsi Agassiz, 1844

This species is known only from the holotype (Moy-Thomas 1935a), which consists of the caudal skeleton, and is distinguished by its large size and high fin-ray count. There appear to be approximately twenty-two rays in each lobe and this is comparable with the caudal fin-ray count of *R. tingleyense*. It is likely therefore that, were more of this specimen known, it would prove identical with that species. At present, however, it must remain coelacanth indet.

Wellburn (1920a) erected six new species of coelacanths from the Better Bed Coal, Lowmoor, Yorkshire, all of which were introduced by name only and no holotypes were designated. Two of these (*C. corrugatus* and *C. granulostratus*) were subsequently described by Moy-Thomas (1935a), the first being placed in synonymy with *R. elegans*, the second being here considered a synonym of *R. tingleyense*. *C. distans*, *C. woodwardi*, *C. spinatus*, and *C. tuberculatus* were names coined for isolated bones which cannot definitely be identified as belonging to a coelacanth.

Rhabdoderma (?) *davisi* Moy-Thomas 1937

and

Rhabdoderma (?) *abdenense* Moy-Thomas 1937

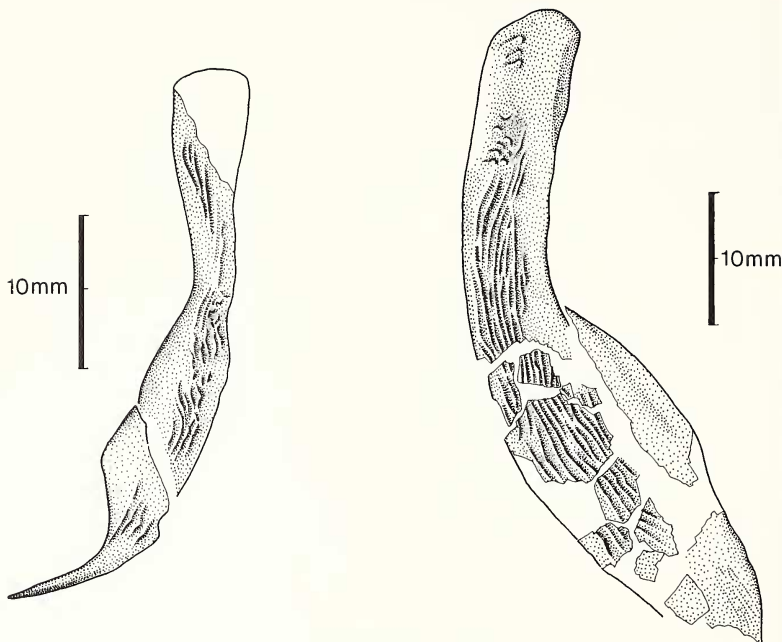
For synonymy of both species see Moy-Thomas, op. cit.

Remarks. Both of these species were erected on isolated head bones. *R.*(?) *davisi* is from the Carboniferous Limestone of Armagh, Ireland, and *R.*(?) *abdenense* from the Calciferous Sandstone of Abden, Fife (Viséan P₁). It is appropriate to discuss these two Lower Carboniferous species together since there is some evidence that they are synonymous and together referable to the genus *Diplocercides*.

In both the British forms the gular plate is ornamented with many fine, parallel striae; the lateral striae curve medially at the anterior end. Such a pattern is also seen in *Diplocercides kayseri* (v. Koenen) (Stensiö 1937, pl. 1) and *D. heiligenstockiensis* (Jessen 1966, pl. 21, fig. 4).

The operculum of *R.*(?) *davisi* is very rounded, as in *Diplocercides*, and the pattern of ornamentation (Moy-Thomas 1937, pl. 4F) is strikingly similar to that of the holotype of *Diplocercides schmidti* Stensiö (Stensiö 1937, pl. 9). The ornament on the operculum of *R.*(?) *abdenense* as figured by Moy-Thomas (1937, pl. 4, fig. A) is very similar to that of the holotype of *D. kayseri* (Stensiö 1937, pl. 1). The difference in ornament between these species of *Diplocercides* may simply be due to individual variation since there are few other distinguishing characteristics. In turn the difference in ornament between the two British species may be due to similar variation.

R.(?) *abdenense* has a large cleithrum upon which the ornament is very pronounced (BMNH P.11077) and consists of parallel ridges which run nearly the entire length of the cleithrum. This is totally unlike the ornament seen in any species of *Rhabdoderma* (text-fig. 7) but is similar to that in



TEXT-FIG. 11. *Diplocercides*—camera-lucida drawings of shoulder girdles. A. Left cleithrum and clavicle of *Diplocercides kayseri* (v. Koenen), specimen 'd' (Stensiö 1937). B. *Diplocercides davisi* (Moy-Thomas), cleithrum of right side, BMNH P.11077.

D. kayseri (text-fig. 11). The marked constriction midway along the cleithrum is also shared by these two species.

In sum, therefore, there are considerable similarities in the ornamentation on the gulars, operculum, and cleithrum between *R.(?) abdenense*, *R.(?) davisi*, and *D. (Nesides)*, sufficient in my view to associate them in the same genus. More complete material of the two British forms would obviously be helpful to substantiate or reject this claim. The scales of *Diplocercides* (see Stensiö 1937) are very different from those of *Rhabdoderma*, and in the caudal fin of the former genus the fin-rays outnumber the endoskeletal supports. The paucity of British material also makes it difficult to associate these with any particular species of *Diplocercides* but they seem most similar to *D. kayseri* (which probably includes *Nesides schmidti*, despite the claims of Stensiö 1937).

For the reasons given above I include *R.(?) abdenense* as a synonym of *R.(?) davisi*, since the latter has page precedence (Moy-Thomas 1937, p. 410) and place them in the genus *Diplocercides* as *D. davisi*. The recognition of a separate species for the Lower Carboniferous forms is solely conservatism pending more complete material. At present this is merely a geographic and stratigraphic species.

During the final stages of the preparation of this manuscript a scale was discovered by Mr. Stanley Wood (Edinburgh) from the Cementstones of Crooked Burn, Foulden, Berwickshire. The horizon, according to him, is equivalent to localities numbered 8, 9, 19 by Schram (1979); that is, lowermost Carboniferous. The scale is 5 mm deep and the exposed surface is covered with closely set ridges which run parallel and do not converge posteriorly. They are similar to those of *D. kayseri*, and it is therefore possible that this is a further record of *Diplocercides* in the Lower Carboniferous.

Coelacanthus sp. (Aldinger 1931)

At this point it is appropriate to mention material described as *Coelacanthus* sp. by Aldinger (1931) from the basal Namurian (E_1 zone) of Westphalia, Germany. This material consists of a few isolated skull bones and scattered axial skeleton remains. The interest of this form centres on the fact that the extensively ossified ethmosphenoid shows a well-developed basiptyergoid process, and this is the source of the assumption that this process is present in all species of *Rhabdoderma*. Moy-Thomas placed Aldinger's *Coelacanthus* sp. as a synonym of *R. (?) aldingeri* although no justification was given. There is indeed no reason to assume that it belongs to this species or even to the genus *Rhabdoderma*. It could belong to *Diplocercides*, with which Aldinger made all his comparisons. The only basis for comparison is the description of the ornament on the operculum, which is said to consist of irregular tubercles anteriorly and parallel ridges posteriorly. This matches the holotype of *D. kayseri* as figured by Stensiö (1937, pl. 1). I therefore recommend that Aldinger's *Coelacanthus* sp. be referred to *Diplocercides*.

CARBONIFEROUS SPECIES FROM OUTSIDE THE BRITISH ISLES

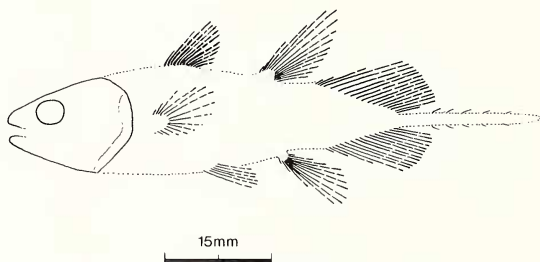
Species of Carboniferous coelacanths have been recorded from northern Europe, eastern Ukraine, North America, and Egypt. Most of these species were originally described as *Coelacanthus* but are more correctly known under *Rhabdoderma*. In this section it is proposed to deal with these species, but for most only a few comments are required, since Moy-Thomas has dealt satisfactorily with many of the European forms.

On mainland Europe *R. elegans* is known from the Namurian and Westphalian coalfields formed along the northern shores of the old Hercynian continent, from northern France in the west to the Donetz basin in the east. In France (Pruvost 1919), Belgium (Demanet and Straelen 1938), Holland (Heide 1943), and West Germany (Keller 1934), *R. elegans* is accompanied by *R. tingleyense*. Precise stratigraphic distribution is given by Keller (op. cit.) for most of these occurrences. Chabakov (1927) records *R. elegans* from late Carboniferous strata (C^0_6 , equivalent to Stephanian B, Kozutskaya, Kosenko, Lipnyagov, and Nemirovskaya 1979) of Izvarino, Ukraine. Chabakov (1927, p. 306, pl. 15, fig. 6) also describes a new genus and species of coelacanth, *Rhomboderma gorskyyi*, from the Upper Carboniferous of the Donetz basin. Both the description and the figures are, in my view, insufficient to allow the material to be identified as coelacanth.

A total of nine species have been described from North America, and these have been referred to three genera. As with the forms from elsewhere, the original species were based largely on slight differences in ornament on opercula, gulars, and scales. *C. elegans*, *C. robustus*, and *C. ornatus* were all described by Newberry (1856) and these, together with *Conchiopsis filiferus* and *C. anguliferus*, both described by Cope (1873), come from the famous Westphalian D deposits of Linton, Ohio. It is clear from a later paper by Newberry (1873a) that he had reservations in using three species names for the Linton coelacanths. *Coelacanthus ornatus* was founded on a single individual much smaller than most in his collection. *C. robustus* was founded on a few individuals much larger than *C. elegans*, which is by far the most common coelacanth at Linton. The slight differences in scale ornament do not stand critical examination with the wealth of material now available, and Moy-Thomas correctly placed them as synonyms of *Rhabdoderma elegans*. *Conchiopsis filiferus* and *C. anguliferus* were very poorly described by Cope from material sent to him by Newberry, who quickly realized (1873b) that

these two species were synonyms of *R. elegans*. So the Linton coelacanth may all be referred to the single species *R. elegans*, which is also the commonest species in Europe.

Coelacanth has been described from Mazon Creek, Illinois (Westphalian D). Hay (1900) records a scale of *Coelacanthus robustus* Newberry, and Eastman (1902) described *C. exiguus*, the latter based on very small individuals. Some of these are now known to have yolk sacs (Schultze 1972) and to be juveniles. The skeleton is very poorly ossified and meristic counts are very difficult to make and seem to vary considerably, probably due to incomplete ossification. The maximum counts are probably more realistic than the average. Two specimens, FM PF 3660 and 7338, both of about 52 mm length (snout-base of the supplementary caudal lobe) show 19 rays in the upper and 18 in the lower lobe of the caudal fin. This count is similar to that in *R. ardrossense*. A maximum of 13 rays can be counted in the anterior dorsal fin of FM PF 7338 and this is comparable with that in *R. tingleyense*; D₂ 15; A 11 (FM PF 3660) and there are 52 neural arches in FM PF 6270, more than in any other species of *Rhabdoderma*. The outline and fin positions (text-fig. 12) are similar to those in *R. elegans* (text-fig. 9) if allowance is made for the juvenile characteristic of a long supplementary caudal lobe, but there is nothing unique to *Rhabdoderma* in these proportions. Neither the shape of the first dorsal fin support, nor the shape or ornament of the scales and head bones, can be seen so the inclusion of this 'species' in the genus *Rhabdoderma* is provisional.



TEXT-FIG. 12. *Coelacanthus exiguus* Eastman. Outline of small individual, FM H.498a + b.

C. newelli and *C. arcuatus* were described by Hibbard (1933) from the late Carboniferous of Kansas. Moy-Thomas considered these as synonyms of *R. elegans*. However, Echols (1963), using much more material, recognized a single form to which she gave the new generic name *Synaptotylus newelli*. She distinguished *Synaptotylus* from *Rhabdoderma* on four main points: the shape and position of the antotic process; the size and position of the basipterygoid process; the shape of the squamosal; and the pattern of ornament on the operculum, suboperculum, and angular.

I have not seen original material of the Kansas form but several aspects of Echols' paper need comment. The antotic process is restored (fig. 1) as a knob-like process directed anteroventrally and finishing close to the ventral margin of the basisphenoid. The process lies below the level of the sphenoid condyles. This, as Echols admits, is unlike the process in *Rhabdoderma* (text-fig. 1) and is, in fact, unlike that of any other coelacanth. It may be questioned whether this interpretation is correct, since apparently only one dorso-ventrally crushed specimen shows the basisphenoid. Certain difficulties arise when one tries to restore the mutual relations of the palate and the braincase using this restored low articulation point between the basisphenoid and metapterygoid. The palate as restored (fig. 4) is like that of *Rhabdoderma*. In life it would have articulated postero-dorsally with the antotic process and anteriorly with the lateral ethmoid by way of an autopalatine, apparently not

preserved in the material of *Synaptotylus*. The anterior tip of the pterygoid (endopterygoid), which is preserved, would presumably lie adjacent to the anterior tip of the parasphenoid as in all other coelacanths. The consequence of restoring the palate in place upon the restored braincase (figs. 1-3), assuming a low position of the antotic process, is to bring the lower jaw articulation beneath the posterior third of the orbit. This is a very unusual position for the jaw articulation in coelacanths; it means that the lower jaw would project considerably beyond the upper, and it is not shown in that position in the restoration of the skull (fig. 3). The usual position of the antotic process is immediately beneath the hind edge of the frontal. If this were the case in *Synaptotylus*, the effect would be to bring the lower jaw articulation back to approximately the position seen in Echols' fig. 3.

The basiptyergoid process is said to be smaller and more laterally placed than that restored in *Rhabdoderma* by Moy-Thomas, and to be continuous with a 'low connecting ridge' (Echols 1963, p. 481) which presumably represents the processus connectens. The 'basiptyergoid process' may simply be the expanded end of the processus connectens (see p. 207 for a discussion of this area in *R. elegans*). The squamosal of *Synaptotylus* is said to be produced ventrally as a small process, and thus differs from the triangular element in *Rhabdoderma*, but the entire outline of that bone is dashed in the restoration (fig. 3), presumably implying uncertainty. The vertebral counts of about fifty neural arches is slightly higher than that recorded for species of *Rhabdoderma*, but the shape and ornament of the scales are said to be similar to *R. elegans*, as is the caudal fin-ray count of twelve rays in both upper and lower lobes. The ornament as described and figured by Echols on the operculum, suboperculum, and angular, is certainly different from that in any other species of *Rhabdoderma*. It consists of short, isolated, and well-spaced tubercles.

In sum, I am sceptical of the basisphenoid restoration and the description of the squamosal given by Echols and, in consequence, of the distinctness of this form. With the exception of the ornament described, other observations support inclusion of *Synaptotylus* in *Rhabdoderma*.

The last of the nine North American species to be mentioned is *C. welleri* Eastman (1908) from Iowa. This form, which is only known from the holotype, is interesting from two points of view. It comes from the base of the Kinderhook Limestone and is therefore of very early Carboniferous age (Tournasian or lowermost Viséan). The specimen, which I have not seen, consists of a scale-covered trunk and the operculum, cheek bones and lower jaw of the right side. Unfortunately Eastman does not describe the ornament in detail, referring the reader instead to a rather poor photograph. But he does mention that the scales on the posterior part of the trunk have fine, *longitudinal* ridges and that the operculum and cheek bones are covered with spiniform ornament which Moy-Thomas likened to that of *R. abdenense*, here referred to *Diplocercides*. I suggest that a closer examination of *C. welleri* and species of *Diplocercides* may allow a more precise identification.

One final note on North American Carboniferous coelacanths should be added. There are several forms now known from the Bear Gulch Limestone (Namurian A) of Montana. One very peculiar form, *Allenypterus montanus*, has been described (Melton 1969) and the rest are to be described by R. Lund and W. Glickman-Lund (pers. comm.).

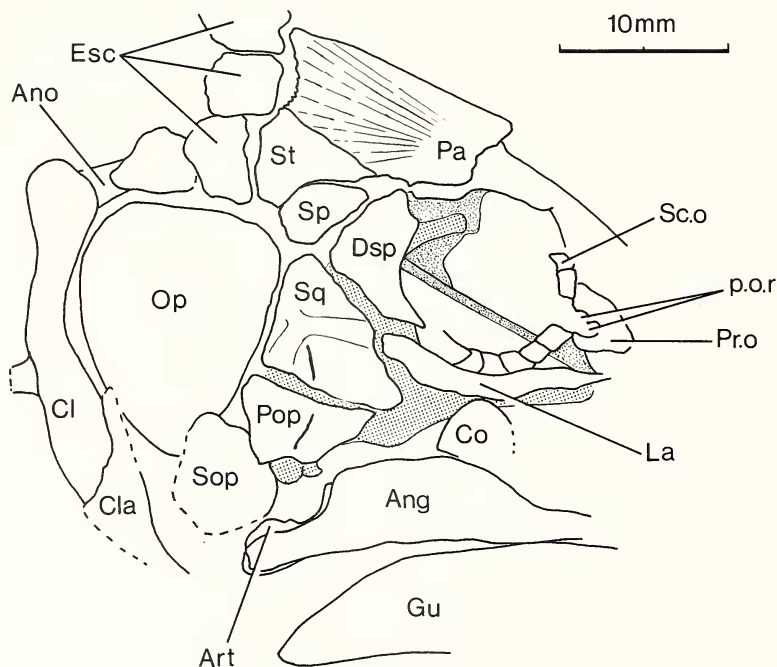
Heide (1955) describes a new species of coelacanth, *Rhabdoderma* (?) *aegyptiaca*, from a marine horizon in the Lower Carboniferous of Egypt. This form is based on isolated scales which are not those of a coelacanth but can be referred to the rhizodontiform *Strepsodus*.

TRIASSIC SPECIES OF *RHABDODERMA*

Rhabdoderma is usually considered as confined to Carboniferous strata, but one form from the southern hemisphere may, with confidence, be referred to the genus. *C. madagascariensis* Woodward is from the Lower Triassic of Andongozo, Madagascar. The original description (Woodward 1910) was enlarged upon by Moy-Thomas (1935b) and both were based on the holotype. These authors stressed the similarity between *C. madagascariensis* and the Coal Measure *Rhabdoderma*, noting particularly the shape and ornament of the scales, the cheek bones, and the position of the pelvic fins. Indeed, the similarity is so great that Moy-Thomas (1937) suggested that *C. madagascariensis* be placed in the genus *Rhabdoderma*, and even questioned whether it came not, from the Lower Triassic,

but from the Permo-Carboniferous as first described (Woodward *op. cit.*). I do not think that the stratigraphic provenance can be in doubt. The holotype is preserved as a natural cast in a nodule typical of the famous fish fauna from the marine Middle Sakamena Group (Dienerian). Another specimen (MNHP 1972-7) is now known, again preserved in a similar nodule.

I agree with Moy-Thomas, and include this species as *Rhabdoderma madagascariensis* (Woodward). The head (text-fig. 13) shows many similarities with other species of the genus; there are five extrascapulars, the cheek bones obviously fitted closely together, the squamosal is the largest of the series, the preoperculum is small, the vertical pitline crosses both the preoperculum and the squamosal, the suboperculum is large and bears ornament similar to that on the scales as in *R. elegans*. The postcranial skeleton, so far as it is known, is also similar to the Carboniferous species in fin positions, and the meristic counts most closely approach those of *R. elegans*: D₁ 10; D₂ 15; C approximately 12 in both upper and lower lobes. The shapes of the anterior and posterior dorsal fin



TEXT-FIG. 13. *Rhabdoderma madagascariensis* (Woodward)—camera-lucida drawing of rubber latex cast of holotype (BMNH P.10768). Abbreviations: Ang—angular, Ano—anocleithrum, Art—articular, Cl—cleithrum, Cla—clavicle, Co—coronoid, Dsp—dermosphenotic, Esc—extrascapular, Gu—gular, La—lachrymal, Op—operculum, Pa—parietal, Pop—preoperculum, p.o.r—posterior openings of the rostral organ, Pr.o—pre-orbital, Sc.o—sclerotic ossicle, Sop—suboperculum, Sp—spiracular bone, Sq—squamosal, St—supratemporal.

supports and the anal fin support are also similar. The ornament on the scales (text-fig. 10) is very similar to that of *R. elegans*, except that the apical tubercles are rounded and close set, although even this pattern is matched in some specimens of *R. elegans* (e.g. Demanet and Straelen 1938, fig. 112).

The body proportions of *R. madagascariensis* differ from those of *R. elegans* (the only other species well known in this respect) in two ways. First, the distance between the first rays of the dorsal fin equals 32% of the length (26% in *R. elegans*). Second, *R. madagascariensis* is a deeper bodied fish with a maximum body depth of 30% body length (cf. 25%). There are also fewer vertical scale rows, about forty compared to fifty-five in *R. elegans*. To these meristic differences may be added the pattern of ornament, which consist of closely packed tubercles of regular size, most closely comparable with the *R. tingleyense*. These meristic features and the pattern of ornament on the operculum are sufficient to maintain specific distinction.

PHYLOGENETIC POSITION OF *RHABDODERMA*

Previous ideas on *Rhabdoderma* are embodied in classifications of coelacanths. These have been essentially gradal (e.g. Romer 1945; Berg 1940; Vorobyeva and Obruchev 1967) and based on characters of the braincase. *Rhabdoderma* has been considered as being at a 'level of organization' (a grade) intermediate between that exemplified by *Diplocercides* and that exemplified by *Coelacanthus*, the Mesozoic coelacanths, and *Latimeria*. *Latimeria* has been placed in a group collateral with the grade groups recognized for the fossil coelacanths (Romer 1945), but this is based solely on the fact that *Latimeria* is a Recent animal. *Laugia* is usually separated from this gradal arrangement by virtue of the forward position of the pelvic fins. It is placed in a monogeneric taxon, equivalent to the gradal taxa.

The 'Diplocercides-grade' is characterized by a well-developed basiptyergoid process and the fact that the ethmosphenoid and otico-occipital moieties of the braincase are each ossified as a single unit. These are both primitive features. The 'Coelacanthus-grade' shows several distinct ossifications in both neurocranial moieties and the loss of the basiptyergoid process. *Rhabdoderma* was presumed to have retained the basiptyergoid process (but see p. 207) but to have a fragmented braincase.

The gradal system of coelacanth classification has been erected largely by using primitive character-states as evidence of relationship, with the result that there is no clear distinction between mono- and paraphyletic groups. The *Diplocercides*-grade cannot be maintained as a monophyletic group since there is no synapomorphy linking *Diplocercides*, *Euporosteus*, and *Chagrinia*. However, it is possible to link *Rhabdoderma* with the rest of the coelacanths by four synapomorphies, numbered 7-10 in text-fig. 14. *Rhabdoderma* does not show synapomorphies 11-20 in the figure. The cladogram shows only a few better-known coelacanth genera, but it does show that the inclusion of *Rhabdoderma* with *Diplocercides* (e.g. Vorobyeva and Obruchev 1967) cannot be maintained.

I see little point in trying to erect a classification to reflect every branching point on this diagram, particularly since several other genera (e.g. *Spermatodus*, *Coelacanthus*, *Winania*, and a new genus from the Eotriassic of East Greenland) have yet to be incorporated. But it is possible to provide a consistent classification using existing ranks and names with the addition of the plesion convention, recommended by Patterson and Rosen (1977). The choice of ordinal rank for coelacanths is arbitrary. Within a cladistic classification of vertebrates as a whole it may be desirable (although it is never necessary) to raise the rank level.

ORDER Coelacanthiformes

plesion *Diplocercides*

plesion Rhabdodermatidae Berg 1940

Rhabdoderma

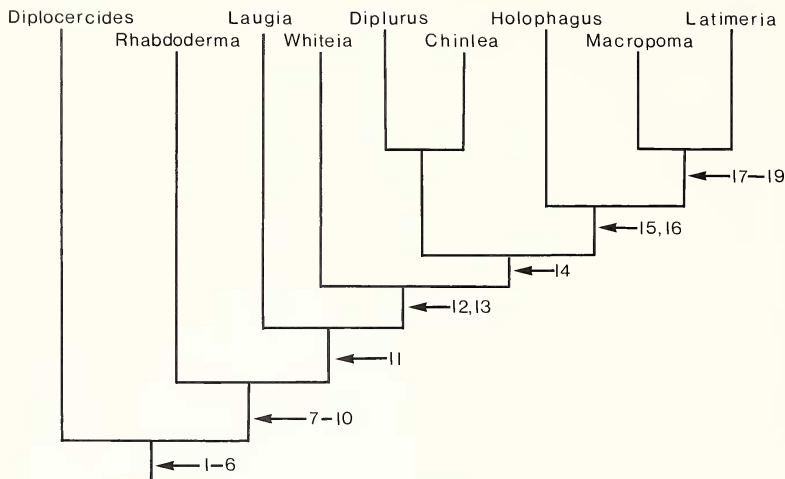
SUBORDER Coelacanthoidei Vorobyeva and Obruchev 1967

FAMILY Laugiidae Berg 1940

Laugia

FAMILY Coelacanthidae Agassiz 1844

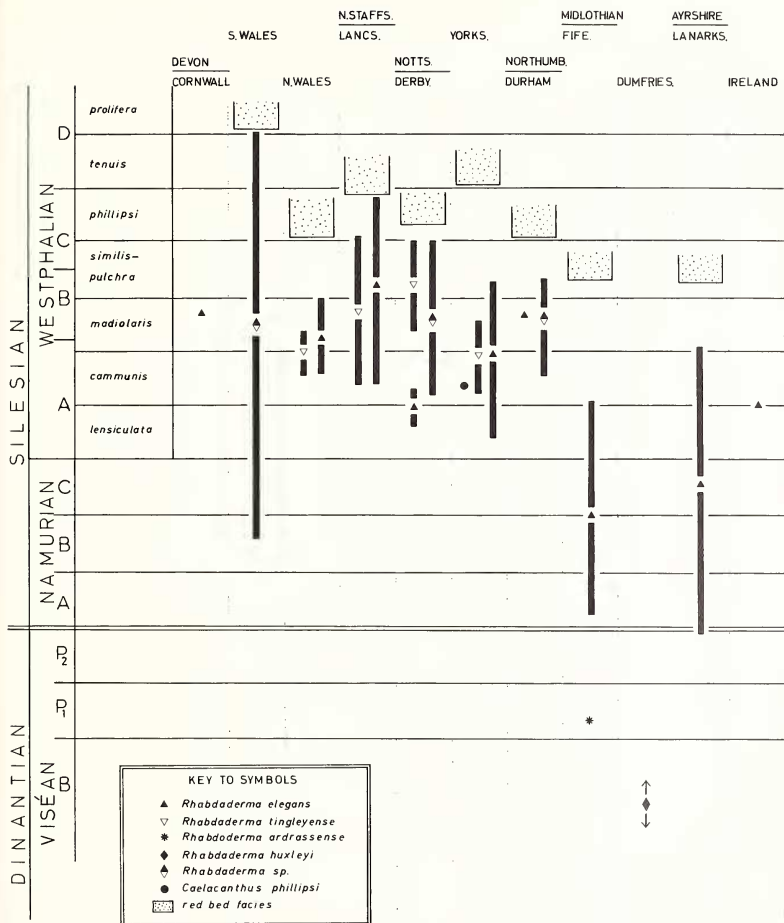
Whiteia, *Diplurus*, *Chinlea*, *Holophagus*, *Macropoma*, *Latimeria*.



TEXT-FIG. 14. Character phylogeny of some of the better-known coelacanth genera. Key to synapomorphies: 1—tandem double jaw articulation, 2—rostral organ, 3—branchiostegals (submandibulars) absent, 4—maxilla absent, 5—supplementary caudal fin, 6—extracleithrum present, 7—basiterygoid process absent, 8—descending process of supratemporal present, 9—caudal fin rays equal in number to internal supports, 10—process of frontal bracing basisphenoid, 11—medial branch of otic sensory canal, 12—posterior lamina outgrowth of prootic, 13—descending process of parietal present, 14—preorbital (antorbital) lost, 15—jugal canal running along ventral margin of squamosal, 16—anterior dorsal laminae on parasphenoid, 17—anterior branches developed from supratemporal commissure, 18—seven extrascapulars, 19—ascending process on prootic.

STRATIGRAPHY AND PALAEOECOLOGY

In the British Isles *Rhabdoderma* is restricted to the Carboniferous, and mainly to the Upper Carboniferous. A chart showing the stratigraphic range of the various species recognized in this paper is presented as text-fig. 15. This chart is compiled from locality and stratigraphic information accompanying specimens examined, and information from numerous regional Memoirs of the Geological Survey of England, Scotland, and Ireland. The raw data, with references, is on file in the Dept. of Palaeontology, B.M. (N.H.). Two qualifying remarks must be made about this chart. First, only those coalfields from which many specimens have been recovered are included; a few specimens have been found outside these areas but their stratigraphic occurrence is included within the data presented here. For instance, isolated scales have been found in borehole samples from the concealed Kent coalfield and from the Shrewsbury and Coalbrookdale coalfields, but their stratigraphic distribution lies within the range of neighbouring coalfields. Second, for some areas, such as the South Wales coalfield, it has not been possible to examine original material, and the literature contains identification only to generic level. In other areas, such as the Notts./Derby and the Northumberland/Durham coalfields, inclusion of only the specimens identified to species would present a very distorted picture, so records of *Rhabdoderma* sp. are included. In all probability this category represents *R. elegans* and *R. tingleyense* only.



TEXT-FIG. 15. Diagram showing stratigraphic range of *Rhabdoderma* species within the major coalfields of the British Isles. See text for further explanation. Position of the red-bed facies from Ramsbottom *et al.* (1978).

The most widely distributed species in both time and space is *R. elegans*, which is known from all areas of coal deposition in the British Isles. On mainland Europe it is known from Westphalian A-C of northern France, Belgium, Holland, and from Namurian B to Westphalian C of the Ruhr coalfields. *R. elegans* is also known from the Stephanian of the Donetz basin. *R. tingleyense* is only slightly more restricted, being unknown from the Scottish Midland Valley coalfields and Ireland. Assuming that the South Wales records of *Rhabdoderma* do not contain this species then, in Britain, it appears to be confined to the Pennine depositional province (Calver 1969, fig. 1). In palaeogeographic terms this is bounded to the south by Wales-Brabant Island and to the north by the reconstructed island extending from Co. Down to Ayrshire (Wills 1951, pl. 9). *R. tingleyense* is also known from Westphalian A of northern France, Belgium, and Holland, and from Westphalian A and B of the Ruhr coalfields.

The temporal pattern of distribution of these two common species of *Rhabdoderma* in Britain and on the Continent matches, in a general way, the pattern of coal distribution and has suggested to some workers (e.g. Westoll 1944) that *Rhabdoderma* is facies controlled. But what particular physical conditions limited the occurrence is by no means clear. Some workers equate Coal Measure fishes with a freshwater existence (Janvier, Termier, and Termier 1979, p. 12) while others (Newberry 1889; Westoll 1944; Schaeffer 1953) believe *Rhabdoderma* in particular to have been restricted to that environment. Further, the coincident disappearance of *Rhabdoderma* and coal-swamp deposition presumably implies preference for a particular type of fresh water. In Britain, red-bed facies, the approximate positions of which are shown on the chart, follow coal deposition. There is, however, a short time span between the disappearance of *Rhabdoderma* and the onset of red-bed régimes. This interval was occupied by fluvial conditions (that is, the relevant beds are represented as coarse sandstones), not by slow moving, near-stagnant coal-swamp waters. Of course due care has to be exercised when considering this 'non-occurrence'. Fossils are rare in these intervening beds and, since there are few productive coals here, the absence may simply reflect a lack of sampling. Be that as it may, the generally held view is that *Rhabdoderma* was a freshwater fish, adapted to the lower reaches of rivers which drained into coal-swamp areas.

Several features of the occurrence of *Rhabdoderma* appear to support this freshwater view. It is found in deposits such as Linton, which is generally held to be a freshwater deposit. Complete specimens are known from blackband ironstones, the Knowles Ironstone of Staffordshire for instance, and these ironstones are sideritic and thus considered to be freshwater deposits. Lastly, *Rhabdoderma* is often found in freshwater mussel bands.

It should be pointed out, however, that *Rhabdoderma* is unknown from the major intermontane freshwater coal deposits, such as Nyirany and those in central France and Spain, and the widespread, almost continuous, occurrence of *R. elegans*, from Illinois to the Ukraine, even allowing for closer proximity of these areas in Carboniferous times, is a distribution rarely seen among freshwater species living today (although Northern Pike and some species of whitefish do show very extensive Holarctic distributions). The widespread distribution of *R. elegans* was accounted for by gradual dispersion through freshwater basins (Newberry 1889), and Westoll invoked a similar explanation for haplolepid. It does, however, seem unnecessary to invoke such large-scale freshwater dispersal. A closer examination of the occurrence of *Rhabdoderma* within the cyclothem deposition of the Lower and Middle Coal Measures shows that it is found in both freshwater and marine horizons (e.g. Culpin 1909; Smith, Rhys, and Eden 1967; Land 1974). Indeed, *Rhabdoderma* is often found in the dark shales overlying coal seams, which are indicative of brackish water preceding fully marine conditions (Calver 1968). On the Continent both *R. elegans* and *R. tingleyense* are found in marine bands within the upper Magerkohle (Wehrli 1931). It is probable that *Rhabdoderma* was, in fact, a euryhaline species, able to move with ease from fresh to sea-water.

CONCLUSIONS

Rhabdoderma is a common coelacanth fish of the Upper Carboniferous of Europe and North America. The stratigraphic distribution matches, with only a few exceptions, the distribution of coal deposits, but several occurrences of *Rhabdoderma* within marine bands suggests that it was a euryhaline fish. The anatomy is best known from the type-species, *R. elegans*. This shows that the braincase is completely ossified in the adult and the presumed ontogenetic sutures have been obliterated. It is unlikely that *Rhabdoderma* retained a basiptyergoid process but is otherwise a primitive coelacanth lacking several synapomorphies which serve to delimit the suborder Coelacanthoidei. It is classified as the primitive sister-group to that taxon.

A large number of species have previously been recognized but here only five are considered valid: *R. elegans*, *R. tingleyense*, *R. luxleyi*, *R. ardrossense*, and *R. madagascariensis*. The last is an early Triassic species. *R.(?) abdenense* is considered to be a synonym of *R.(?) davisi* and, in turn, this species should be referred to the genus *Diplocercides* because of a similar ornament pattern on the operculum, gulars, and shoulder girdle. *C. welleri*, a lower Carboniferous form from Iowa, may also belong to *Diplocercides*, as does *Coelacanthus* sp. (Aldinger 1931). *C. exiguus* is a juvenile form from Mazon Creek. Like *C. hindi* and *C. curta* it must remain as coelacanth indet.

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